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Review Article

An Overview of Dichogamy in Angiosperms

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Dichogamy refers to maturation of sex organs in plants at different times. It has been monitored in plants for over 250 years. It is not a simple process and has many aspects. It is widespread in angiosperms and mainly divided in two main types; proterandry and proterogyny. In degree it may be partial (incomplete) or complete. Dichogamy may be intrafloral or interfloral. In former, it is expressed within a flower, in latter, it exists among flowers in diclinous species. It can be interpreted as a floral mechanism favouring cross-pollination. Proterandry and proterogyny are safeguards against self-pollination. In this review, we discussed patterns of occurrence and importance of dichogamy in the light of previous studies.

Keywords: Dichogamy, Types of Dichogamy, Proterandry, Proterogyny, Function of Dichogamy

Dichogamy is the maturation of male and female reproductive organs at different times in the course of reproduction period of a plant (Lloyd and Webb, 1986). In other words, it refers to anther dehiscence and pollen release occurring at different time than the attainment of receptivity of stigma in a flower of a species or among different flowers in diclinous species (Bertin, 1993; Bertin and Newman, 1993).

Dichogamy was first described by Kölreuter in 1761-1766 (Knuth, 1906). However, Sprengel was the first to introduce this term in the literature in 1793 (Stout, 1928). Sprengel (1793) used the term dichogamy to describe the maturation of male and female sex organs of a hermaphrodite flower at different time intervals.

'Dicho' means in two pieces/separated and 'gamous' means marriage/mating in Greek, and these two words have been combined by Sprengel (1793) (Lloyd and Webb, 1986). A few investigators, mainly Delphino (1868-1874), accepted dichogamy as a general mechanism that requires cross-pollination or a physiological and morphological adaptation to provide cross-fertilization of a flower. However, the currently adopted use of dichogamy is consistent with the definition used by Sprengel (1793) and refers to reproductive activities of two mature sexes represented by the stamen and pistil that occur at different times (Stout, 1928).

Dichogamy commonly exists among angiosperms (Bertin and Newman, 1993). This indicates the important role of dichogamy in floral biology. However, it has drawn less intention compared to other floral features (Lloyd and Webb, 1986). Types, reasons and outcomes of dichogamy have been investigated in a limited number of theoretical and experimental investigations. Lloyd and Webb (1986) associated the negligence regarding dichogamy with the limited attention drawn to the feature by Darwin (1876-1888) compared to other subjects.

Types of Dichogamy

There are several different types of dichogamy which may be evaluated independently. By taking into account the previous definitions by Stout (1928) and Faegri and Pijl (1979); Lloyd and Webb (1986) have grouped dichogamy in 5 distinct classes, and this classification is presented in Table 1.

Table 1. Classification of dichogamy subtypes (Lloyd and Webb, 1986).

Types of Dichogamy				
By the order of presentation	**By floral elements**	**By the degree of stamen and pistil separation**	**By the degree of plant synchronization**	**By the time interval Between stamen and pistil emergence**
1.Proterandry 2.Proterogyny	1. Intrafloral 2. Interfloral	1. Complete 2. Incomplete	1. Asynchronous 2. Hemi-synchronous 3. Synchronous a. Multiple cycles b. Duodichogamy c. Single cycle d.Heterodichogamy	Different time intervals

Two or more subtypes of dichogamy may be present in a plant in a combined manner. Each subtype and each combination may provide different advantages and disadvantages for the plant.

Dichogamy has two main subtypes (Routley, Bertin and Husband, 2004). When the stamen gains reproductive maturity much before the stigma of the same flower attains receptivity in a bisexual flower, it is defined as proterandry (Honek, 1997; Morbey and Ydenberg, 2001) (Table 2). In contrast, when the pistil gains reproductive activity much before the anther dehisces in a hermaphrodite flower, it is defined as proterogyny (Honek, 1997; Buck, 2001) (Table 2). These two conditions have been known as male-female sequence (dichogamia androgyna) and female-male sequence (dichogamia gynandra) for years and were then redefined by Hildebrand (1867) as protandry and protogyny. These two terms were then re-named as proterandry and proterogyny by Delphino (1868-1875) (Stout, 1928).

Concurrent gain of reproductive activity of the stamen and pistil in a hermaphrodite flower may be defined as homogamy (Lloyd and Webb 1986); however, homogamy is not a well-established concept. Faegri and Pijl (1979) have concluded that homogamy is an unimportant term. Consistent with the view of Faegri and Pijl (1979), Lloyd and Webb (1986) suggested the use of adichogamy instead of homogamy. When the stamen and pistil of a hermaphrodite flower attain reproductive maturity at the same time, it translates into absence of dichogamy, and Lloyd and Webb (1986) therefore defined adichogamy as the absence of dichogamy (Table 2).

Dichogamy may be seen in a particular flower of a species as well as among flowers of different individuals from different sexes of the same species (Bertin, 1993; Bertin and Newman, 1993). Attainment of reproductive maturity in the stamen and pistil at different times may exist in a single hermaphrodite flower or among flowers of dioecious or monecious species (Lloyd and Webb, 1986). Intrafloral dichogamy is defined as the gain of reproductive activity at different times in the stamen and pistil of a single hermaphrodite flower. Interfloral dichogamy is defined as the gain of reproductive activity at different times in the stamens and pistils of male and female flowers on different plants in dioecious or on the same plant in monecious with

pistillate and staminate flowers (Lloyd and Webb, 1986).

While intrafloral and interfloral dichogamy may be present in an individual (Lloyd and Webb, 1986), it may also be combined with proterandry or proterogyny. These combinations are termed as intrafloral proterandry, intrafloral proterogyny, interfloral proterandry and interfloral proterogyny (Routley, Bertin and Husband, 2004). Each combination may provide different advantages and disadvantages for the plant.

Development and attainment of reproductive maturity in sex organs can be detected by different conditions. While gain of reproductive maturity in stamen is expressed as anther dehisce and pollen release, gain of reproductive activity in the pistil may be expressed in the formation of receptive surface which frequently consist of elongated papillae, as in *Helianthus annuus* L.. The two branches of stigma in sunflower are attached and contain a limited amount of short papillae in the early stages of floral development. However, when stigma reaches maturity to accept pollen grains, two branches of the stigma are covered with extensive, long papillae (Gotelli *et al.*, 2008, Çetinbaş ve Ünal, 2012). This situation of the stigma is an indicator of the onset of reproductive activity in the pistil.

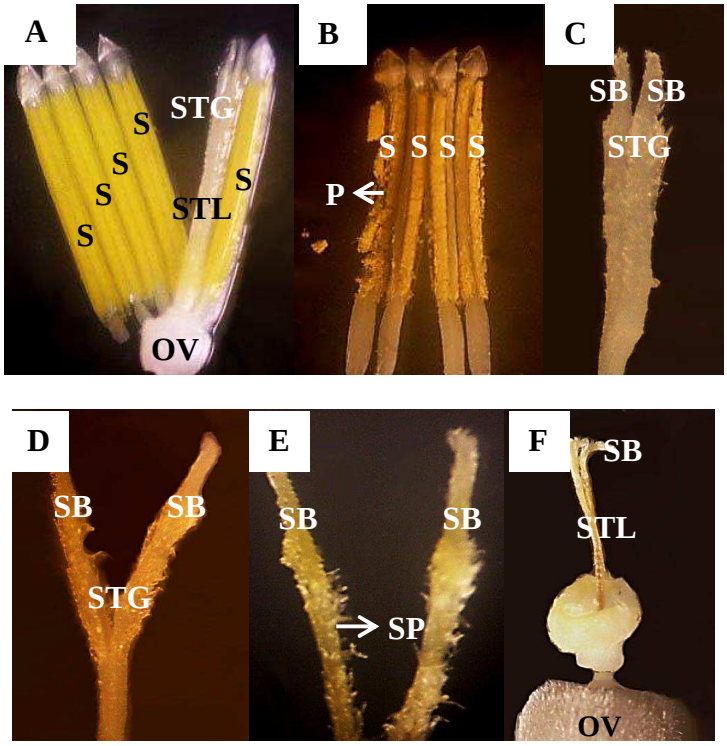


Figure 1. Intrafloral proterandry in hermaphrodite flowers of *H. annuus* L. in stereomicroscopic analysis. A. Male phase: Mature stamens at reproductive activity and unmatured pistil. Stigma and style are transparent-white, indicating an early stage of development. B. Pollen at shedding. C. Stigmatic branches are attached. D. Female phase: Stigma with two branches. E. Stigmatic branches covered by extended papillae. F. Terminated reproductive activity at stamens fallen off the flower. Pistil with swollen ovary and mature stigma (Çetinbaş and Ünal, 2012). S: Stamen, STG: Stigma, STL: Style, OV: Ovary, SP: Stigmatic papillae, P: Pollen, SB: Stigmatic branches.

In protandrous dichogamy, the stamen gains reproductive activity much before the stigma of the same flower attains receptivity and anther dehisce and pollen grains are shed. By the time the pollen reach maturity, the stigma loses receptivity.

Therefore self-pollination is not possible. This may be defined as the male phase. *H. annuus* L., which exhibits protandrous dichogamy, has hermaphrodite flowers that initially enter the male phase, followed by the female phase (Çetinbaş and Ünal, 2012). The histological sections of the hermaphrodite floral buds of *H. annuus* L. revealed that stamen primordia derived from floral meristem before pistil primordia (Figures 2.A, 2.B) (Çetinbaş and Ünal, 2012). During the stages when the pollen grains are produced, in other words when the stamen has gained reproductive activity (Figure 1.A, 1.B, 3.A, 3.B, 4.A), the sections reveal the newly appearing ovule, and the stigma is yet to divide into two pieces, which means that the pistil has not gained reproductive activity (Figures 1.C, 4.B). The stigma therefore does not accept pollen. During the subsequent stages when the embryo sac is formed in the ovule as stigmatic branches appear and the stigma papillae to accept pollen in style clearance become apparent (Figure 1.D, 1.E, 3.C, 4.C, 4.D), pollen mostly lose the ability to germinate. Stamens shrivel and may have fallen off the flower (Figure 1.F, 3.D) (Çetinbaş and Ünal, 2012).

The proterandry is at the intrafloral level in the hermaphrodite flower of *H. annuus* L.. In other words, the stamen reaches maturity before the pistil in each individual hermaphrodite flower of *H. annuus* L. (Figures 1.A-F). This is termed as intrafloral dichogamy. The SEM analysis of protandrous hermaphrodite flowers of *H. annuus* L. indicate that stigmatic branches remain attached without extending out from the tube formed by the anthers during the stages when pollen grains are located in pollen sacs (Figures 4.A, B) (Çetinbaş and Ünal, 2012). By the time the stigmatic branches start widening and the female organ gains reproductive activity, stamens lose their reproductive activity and filament folding starts, indicating that stamens are to fall off from the flower (Figure 4.C). The lengths of stigmatic papillae are remarkable during this period (Figure 4.D).

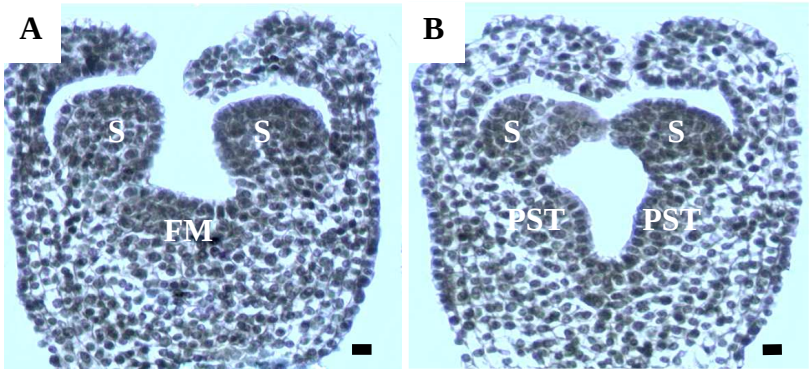


Figure 2. The histological sections of proterandrous hermaphrodite floral buds of *H. annuus* L.. Male organ primordia are formed before that of female organ. A. Stamen primordium is the first primordium derived from the floral meristem. B. Pistil primordium is formed after an interval following the formation and elongation of stamen primordia. This partially explains how the male function precedes the female (Çetinbaş and Ünal, 2012). S: Stamen, FM: Floral meristem, PST: Pistil. Bar: 10 µm.

The stamen and pistil gain reproductive activity at different times in dichogamy. In complete dichogamy, the reproductive activity of the stamen and pistil does not occur at the same in a hermaphrodite flower or on different plants in dioecious or on the same plant in monecious with pistillate and staminate flowers. The temporal segregation of stamen and pistil functions is actually complete. In complete dichogamy, the hermaphrodite flower initially enters the male phase and then enters the female phase only when the first phase is

complete, and vice versa (Table 2). This leads to substantially decreased self-ertilization. For example, *Polyalthia hypoleuca* exhibits complete protogyny (Rogstad, 1994).

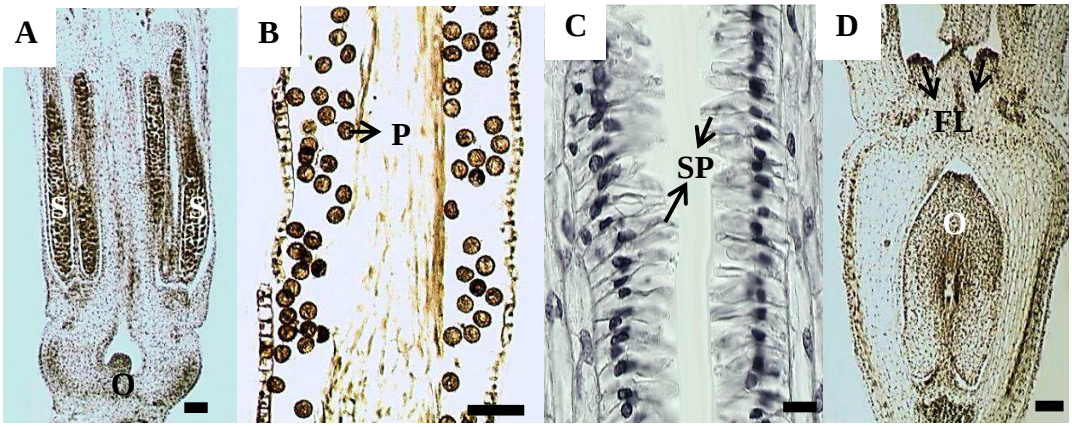


Figure 3. Proterandry in the histological sections of hermaphrodite flowers of *H. annuus* L.. A. Male phase: Mature stamens are at reproductive phase, the ovule newly appeared. B. Mature pollen grains are ready to shed. C. Female phase: Extended stigmatic papillae covering stigmatic branches. D. Mature pistil with embryo sac within the ovule. Stamens fallen off the flower (Çetinbaş and Ünal, 2012). S: Stamen, O: Ovule, P: Pollen, SP: Stigmatic papillae, FL: Filament links. Bar: 10 µm.

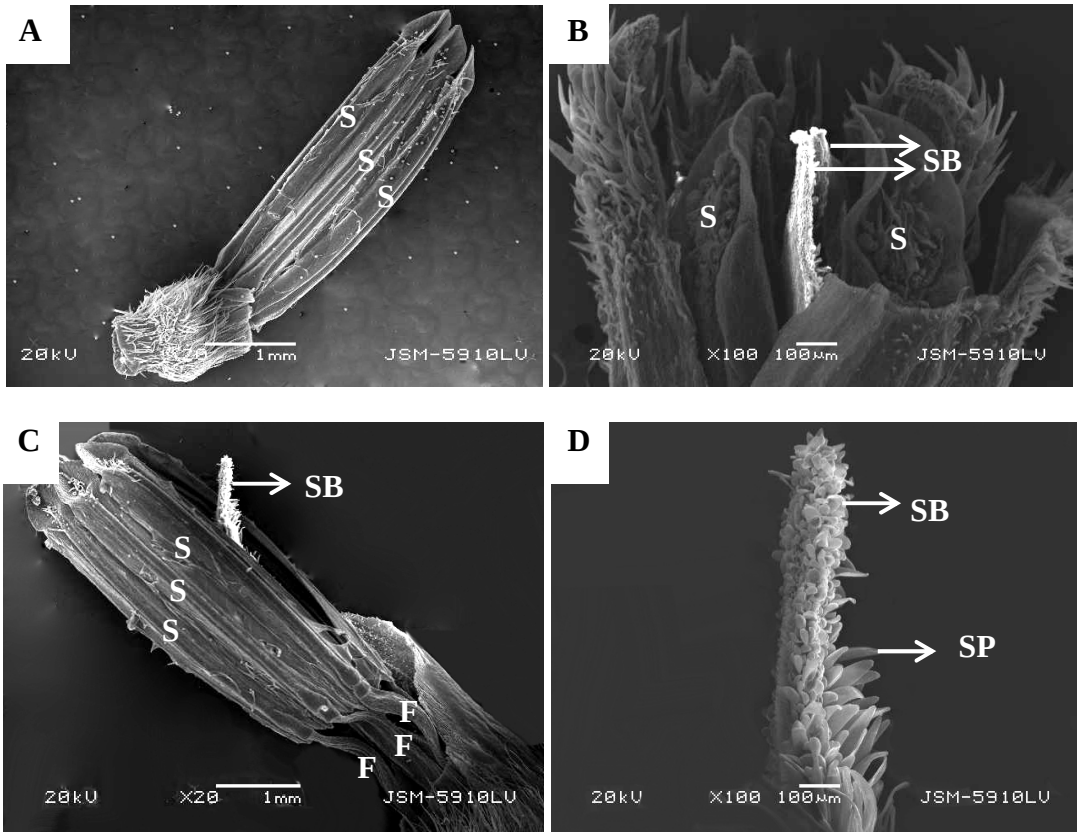


Figure 4. Proterandry in hermaphrodite flowers of *H. annuus* L. in SEM analysis. A. Male phase: The stamens at reproductive activity and pollen shedding. B. Undivided stigma with short papillae. C. Female phase: Pistil at reproductive activity, stigma with two branches starting extending out from the tube formed by anthers. Stamens are near to fall. D. Elongated stigmatic papillae covering the stigmatic surfaces. (Çetinbaş and Ünal, 2012). S: Stamen, SB: Stigmatic branches, F: Filament, SP: Stigmatic papillae.

In protogynous dichogamy, female function precedes. In the flowers of *Aristolochia* the stigma is divided into branches and attain receptivity, however no pollen release occur simultaneously (Figure 5.A). The stigma loses receptivity by the time the anthers dehisce and stigmatic branches are situated in their closed form (Figure 5.B).

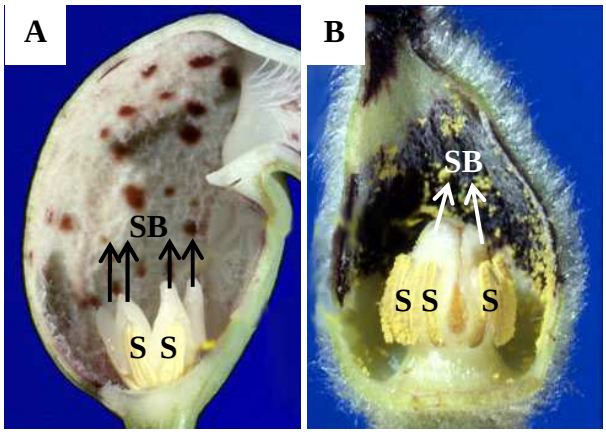


Figure 5. Stereomicroscopic analysis of proterogyny in *Aristolochia*. A: Female phase: Mature pistil with branched stigma and immature stamens B: Male phase: Pollen grains at shedding, stigmatic branches are closed (with permission of Robertson and Nickrent). S: Stamen, SB: Stigmatic branches.

However, in some cases the reproductive activity of the stamen and pistil may overlap during a certain period of time (Table 2). This is termed as incomplete dichogamy (Lloyd and Webb, 1986). The rate of self-fertilization increases in both cases compared to complete dichogamy. Complete and incomplete dichogamy is accompanied by proterandry or proterogyny in a flower and these conditions are termed as complete proterandry, complete proterogyny, incomplete proterandry and incomplete proterogyny.

In the hermaphrodite flower *H. annuus* L. which exhibits proterandry, the reproductive activity of the stamen and pistil overlap for a very limited period of time. This temporal overlap usually occurs before the stamens lose their reproductive functions. When the stamens become profoundly black and approach the end of their reproductive activity, stigma have just started to divide into branches and the pistil has newly gained reproductive activity (Figure 6). Therefore, the stamens and pistil concomitantly exhibit reproductive activity for a short period of time (Çetinbaş and Ünal, 2012). In subsequent stages, the stamens approach the end of maturity, lose their functions entirely and fall off from the flower.

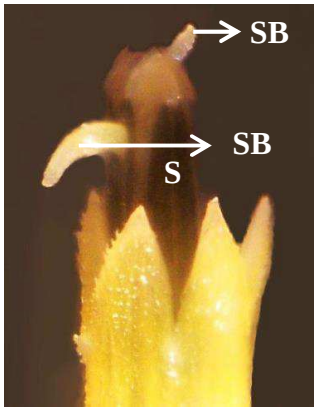


Figure 6. Stereomicroscopic analysis of incomplete proterandry in the hermaphrodite flower of *H.annuus* L.. Stamens blacken at the end of reproductive activity and newly active pistil with two branched stigma. The stamens and pistil simultaneously exhibit reproductive activity for a short period of time (Çetinbaş and Ünal, 2012). S: Stamen, SB: Stigmatic branches.

Dichogamy may be grouped in various classes considering the synchronization of the flowers. The most common form is asynchronous dichogamy (Bawa, 1983; Ims, 1990) (Table 2). In this case, pollen release in the flowers and the pollen acceptance phase of stigma occur at different times in each individual hermaphrodite flower or on influorescence of a plant. For example, *Origanum syriacum* presents asynchronous dichogamy, there is no synchrony between the male and female phases of flowers of a given plant (Riano and Dafni, 2006).

Hemi-synchronous dichogamy is a partial synchronization existed in a few or more flowers or in only a portion of inflorescence (Table 2). In hemi-synchronous dichogamy while there is synchronization among the sex organs of the relevant flowers, there is no synchronization between these flowers and the sex organs in the rest of flowers.

In *H. annuus* L., the blooming continues from the outer whorls of the capitulum and all of the flowers in a given whorl bloom at the same time (Hernandez and Green, 1993; Çetinbaş and Ünal, 2012). In other words, blooming in a given whorl occurs in a synchronized manner along with all the other flowers in the whorl, and all of the sex organs of the flowers in the whorl exhibit the same reproductive stage. However, the flowers in this whorl are not synchronized with the flowers in the other whorl. This translates into a partial synchronization observed in a portion of the capitulum. Hemi-synchronous dichogamy may be combined with proterandry and proterogyny (Thien *et al.*, 1985; Kubitzki and Kurz, 1984).

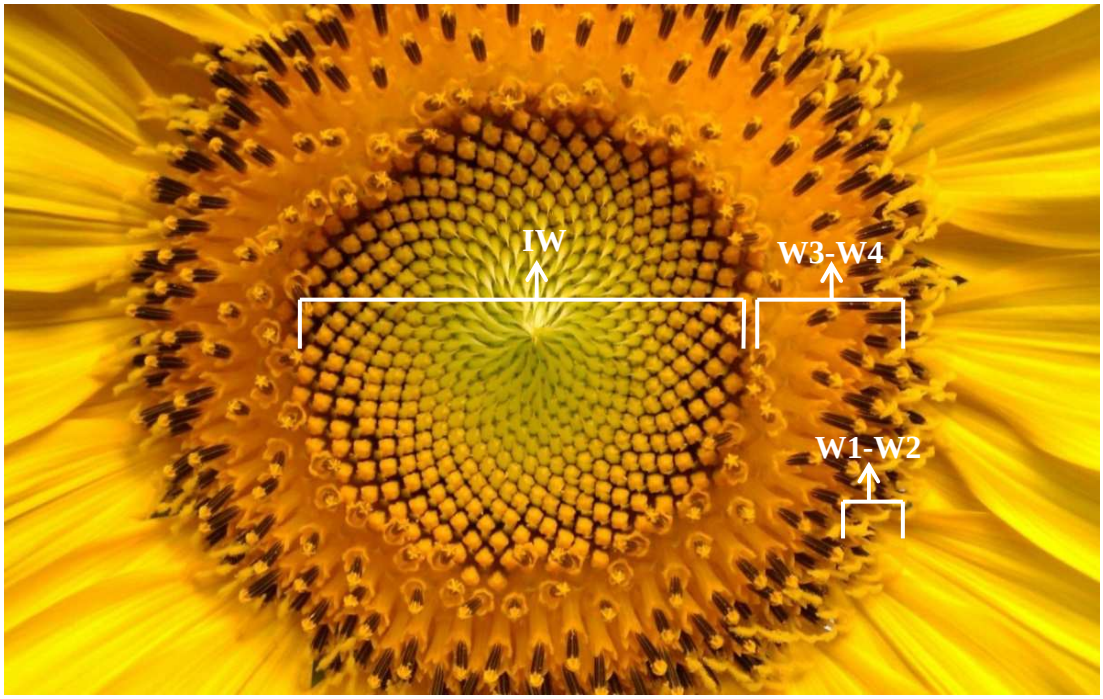


Figure 7. Hemi-synchronous proterandry in hermaphrodite flowers on *H. annuus* L. capitulum. Blooming starts earlier in the outer whorls 1 and 2 of the capitulum (W1-W2). After they completed male phase they enter female phase. Stigma is divided into two branches in the flowers of W1-W2. All of the flowers in outer whorls 3 and 4 are in the male phase. In the innerwhorls, blooming do not start (URL-1). IW: Inner Whorls, W1-W2: Whorl 1 and Whorl 2, W3-W4: Whorl 3 and Whorl 5.

Because floral development has started earlier in outer whorl 1 and 2 (W1-W2), these flowers have completed the male reproductive phase and entered the female

reproductive phase, and all of the flowers in this whorl are at the same stage (Figure 7). In the flowers of outer whorl 3 and 4 (W3-W4), the anthers have reached maturity; however, no segregation is observed in stigmatic branches. Therefore, all of the flowers in these whorls are in the stamen reproductive phase. Blooming in the inner whorls (IW) are not observed simultaneously. In summary, all of the flowers in a given whorl on the capitulum enter the stamen or female organ reproductive stage concurrently without any synchronization between the inner and outer whorls. This partial synchronization is a proof of hemi-synchronous dichogamy in *H. annuus* L. (Çetinbaş and Ünal, 2012). Furthermore, because all of the hermaphrodite flowers of *H. annuus* L. are protandrous, this may also be defined as hemi-synchronous proterandry.

In synchronous dichogamy, all individual flowers in a plant or on an inflorescence are at the same stage at the same time (Table 2). This translates into full synchronization. There are a few subclasses of synchronous dichogamy and this classification is based on the number of cycles in flowers and the genetic features of the flowers. This refers to the switch from the male phase to the female phase or from the female phase to the male phase. In multi-cycle dichogamy, the hermaphrodite flowers in a plant enter multiple consecutive cycles during a florescence season (Table 2). This is the most common form of synchronous dichogamy. The cycle may be protandrous as seen in *Aralia hispida* (Thomson and Barrett, 1981) or protogynous as seen in *Ourisia lactea* (Thien *et al*., 1985).

Duodichogamy was discovered by Stout (1928) in *Castanea* is the second from of synchronous dichogamy and consists of 1.5 cycles during a florescence season (Table 2). 1.5 cycles refers to consecutive switches between 3 different phases. This cycles is usually in the form of male phase-female phase-male phase as seen in *Bridelia tomentosa* (Lloyd and Webb, 1986).

In single-cycle dichogamy, all pollen grains in a plant are released by the time the pistil reaches maturity, or vice versa (Table 2). In other words, only one cycle occurs in the form of male to female or female to male. For example, *Alnus glutinosa* firstly enter the female and the later, male phases (Lloyd and Webb, 1986). It is the second most common form of synchronous dichogamy after multi-cycle dichogamy (Lloyd and Webb, 1986).

Heterodichogamy is the least common form of synchronous dichogamy and has two genetic variants. Heterodichogamous species include two types of hermaphrodite flowers: protandrous and protogynous (Lloyd and Webb, 1986; Stout, 1928). During a time of blooming the first type of flower remains in the male phase while the second type of flower is in the female phase. In other words, the pollens grains initially gain activity in some of the flowers whereas stigma is the first to gain activity in others during a time of blooming (Table 2). This system is known in only 18 genera of 11 families (Delpino, 1874; Gleeson, 1982; Renner, 2001; Endress and Lorence, 2004). For example, *Kingdonia uniflora*' s flowers are heterodichogamous, with protandrous and protogynous morphs (Wang *et al*., 2012).

The subtypes of dichogamy in hermaphrodite flowers are schematically described in Table 2 according to different nomenculature.

The time to reproductive phases in the stamen and pistil, i.e. the time interval of the switch between two different phases demonstrate a wide range of variation. In some cases, particularly in one-day flowering plants, this duration may be a few minutes (Beddows, 1931; Shehbaz, 1977), or a few hours (Primack, 1985), days (Müller, 1883; Cruden and Hermann-Parker, 1977; Galil and Zeroni, 1967; Stout, 1927), weeks (Jong, 1976; Wiebes, 1979, Janzen, 1979) or months (Condon and Gilbert, 1984). In extended florescence season, it may even last up to one year and flowers may remain male for one year and female during the subsequent year

(Charnov and Bull, 1977; Lloyd and Bawa, 1984). The switch from the male phase to female phase in protandrous flowers of *H. annuus* L. may last for a few days or in some cases last up to one week (Çetinbaş and Ünal, 2012).

Dichogamy and Prevalence of Dichogamy Types

Dichogamy is commonly seen among angiosperms (Lloyd and Webb, 1986; Barrett, 2003). Bertin and Newman (1993) clarified different types of dichogamy in 3716 species out of 4277 (approximately 87%) in a literature review (Sargent, Mangedar and Otto, 2006). This rate is not surprising considering the frequent prevalence of dichogamy in hermaphrodite plants and the high rate of hermaphroditism among angiosperms.

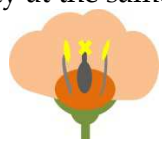
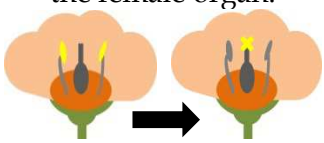
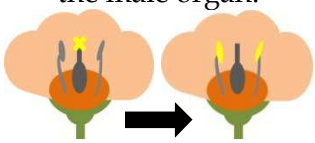
Usually, a plant family is either entirely protandrous or protogynous, or adichogamous (Bennett, 1870). For example, all of the species (apart from a few exceptions) in Compositae family to which *H. annuus* L. belongs, have protandrous flowers. In some exceptional families, intermediate cases may be seen. Furthermore, proterandry, proterogyny and adichogamy may coexist in a family.

Proterandry is more common than proterogyny (Bennett, 1870). In 1881, Thomson conducted a study on 235 hermaphrodite species in New Zealand, and found 105 dichogamous species, 87 of which were protandrous and 18 were protogynous. Proterogyny is considered as an ancestral feature among angiosperms (Endress, 2010) and is therefore more common in primitive angiosperms.

Henslow (1888), Willemstein (1987), Wyatt (1983), Faegri and Pijl (1979) have suggested a mechanistic explanation for the prevalence of proterandry. They estimated that intrafloral proterandry reflects the natural centripetal development and is therefore more commonly widespread. The centripetal development in hermaphrodite flowers of *H. annuus* L. and their protandrous nature may contribute to this approach.

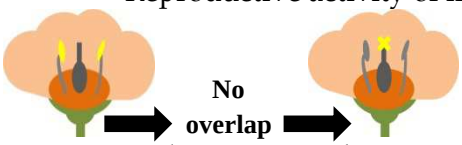
The prevalence of proterandry and proterogyny varies at intrafloral and interfloral levels. While proterandry is more prevalent at intrafloral level, the feature at interfloral level is quite the opposite. Proterandry occurs in 62% of 3151 species with intrafloral dichogamy, and proterogyny exists in 33.8%. 77.9% of 565 species with interfloral dichogamy are found to be protogynous (Bertin and Newman, 1993).

Table 2. Schematic description of dichogamy subtypes in hermaphrodite flowers according to different nomenculature (yellow indicates reproductive activity).

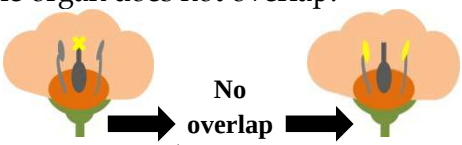
Schematic Description of Dichogamy Subtypes		
Adichogamy Male and female organs gain reproductive activity at the same time. 	**Proterandry** Male organs gain reproductive activity before the female organ. 	**Proterogyny** Female organ gains reproductive activity before the male organ. 

Complete dichogamy

Reproductive activity of male and female organ does not overlap.



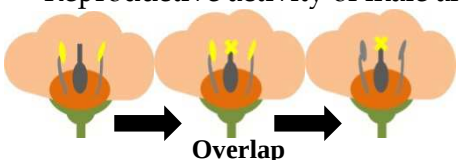
Complete proterandry



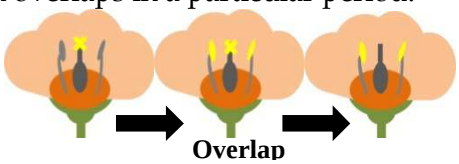
Complete proterogyny

Incomplete dichogamy

Reproductive activity of male and female organ overlaps in a particular period.



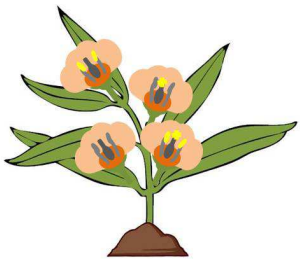
Incomplete proterandry



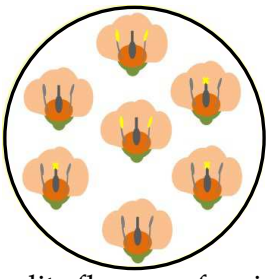
Incomplete proterogyny

Asynchronous dichogamy

Male and female organs gain reproductive activity at different times on each hermaphrodite flower of a plant or on inflororescence of a plant. There is no synchronization.



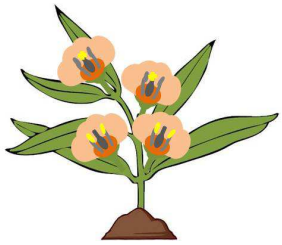
Hermaprodite flowers of a plant



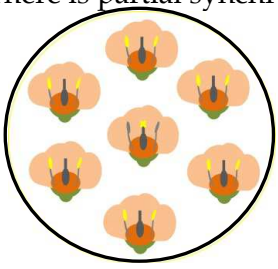
Hermaprodite flowers of an inflourescence of a plant

Hemi-synchronous dichogamy

Male and female organs gain reproductive activity at the same time in a proportion of flowers or in inflourescences. There is partial synchronization.



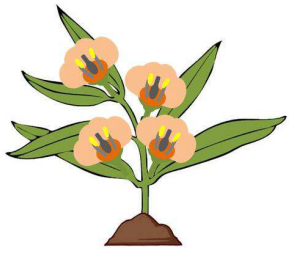
Hermaprodite flowers of a plant



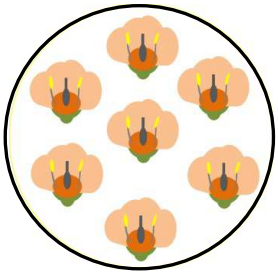
Hermaprodite flowers of an inflourescence of a plant

Synchronous dichogamy

Male and female organs gain reproductive activity at the same time in all of the flowers or in inflourescences in a synchronized manner on a plant.



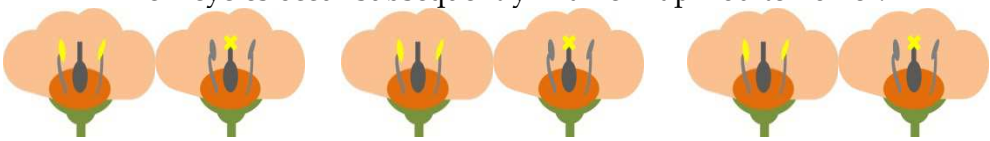
Hermaprodite flowers of a plant



Hermaprodite flowers of an inflourescence of a plant

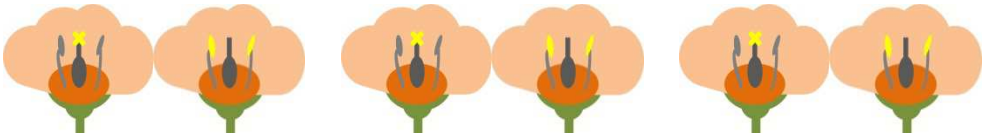
Multiple cycle-dichogamy

A few cycles occur subsequently in a hermaphrodite flower.



1st Cycle 2nd Cycle 3rd Cycle

Multiple cycle-proterandry



1st Cycle 2nd Cycle 3rd Cycle

Multiple cycle-proterogyny

Duodichogamy

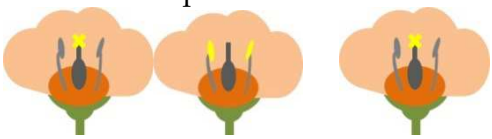
1 ½ cycles occur in a hermaphrodite flower.

1st Cycle ½ Cycle

Duoproterandry

Duodichogamy

1 ½ cycles occur in a hermaphrodite flower.

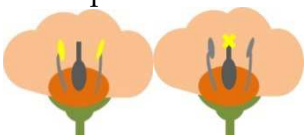


1st Cycle ½ Cycle

Duoproterogyny

Single cycle-dichogamy

A single cycle occurs in a hermaphrodite flower.

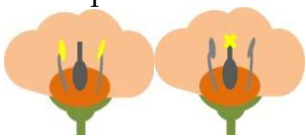


1st Cycle

Single cycle-proterandry

Single cycle-dichogamy

A single cycle occurs in a hermaphrodite flower.

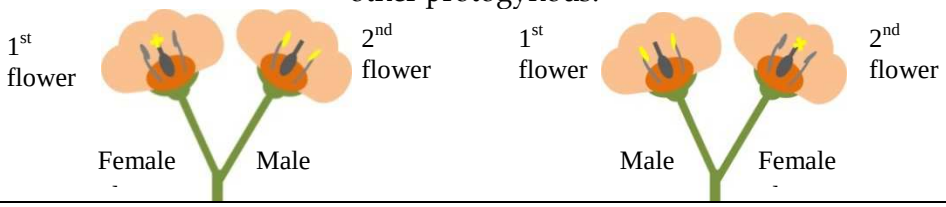


1st Cycle

Single cycle-proterogyny

Heterodichogamy

Two types of hermaphrodite flowers are present on a plant, one protandrous, and the other protogynous.



The rates of proterogyny and proterandry are also interesting among monocots and dicots. At intrafloral level, proterogyny is more prevalent in monocots compared to dicots. While 69.4% of monocots are protogynous at intrafloral level, only 28.8% of dicots are protogynous at this level (Bertin and Newman, 1993). At interfloral level, 73% of monocots and 81% of dicots have been found to be protogynous (Knuth, 1906-1909; Lloyd and Webb, 1986). Primitive classes of dicots are almost always protandrous. In contrast, highly evolved subclasses exhibit high rates

of proterandry. Jones (1939), Percival (1965), Carlquist (1976), Faegri and Pijl (1979) have also reported the prevalence of proterandry among evolved families. *H. annuus* L. belongs to Compositae family, which is also an evolved family, and proterandry is commonly seen among the members of this family.

Some investigators have emphasized the association between dichogamy and flower size. Dichogamy is more common in plants with large flowers compared to those with small flowers (Henslow, 1888), therefore the flowers of dichogamous species are usually larger than adichogamous flowers (Bertin and Newman, 1993). Wilson (1878) reported that large and attractive flowers tend to be protandrous. The protandrous, hermaphrodite flowers of *H. annuus* L. are of approximately 15-20 mm with a bright yellow color and a rather spectacular appearance, supporting this approach (Çetinbaş and Ünal, 2012). Proterogyny on the other hand, is more common among plants with small flowers and those with early florescence (Henslow, 1888). The findings of Bertin and Newman (1993) are consistent with the assumption of Müller (1883) and Henslow (1888) suggesting an association between proterandry and small, nonstriking flowers.

Particularly one-day flowering plants are likely to be protandrous (Bawa and Beach, 1981). This is associated with the non-functional female phases of flowers in one-day proterogyny unless pollinators carry a substantial amount of pollens from the previous day.

Incomplete dichogamy is more common that complete dichogamy (Stouth, 1928) and asynchronous dichogamy is seen more frequently compared to synchronous dichogamy (Bawa, 1983; Ims, 1990). Synchronous and hemi-synchronous dichogamies are usually seen in plants that carry their flowers in the form of a single flower. The hermaphrodite flowers of *H. annuus* L. which exhibit hemi-synchronous dichogamy are also located on inflorescence in the form of a capitulum. Furthermore, *H. annuus* L. belongs to the Compositae family where synchronous and hemi-synchronous dichogamies are commonly seen. The most common form of synchronous dischogamy is the multi-cycle dichogamy. The least common form, heterodichogamy is known to be present only in a few taxons among angiosperms (Renner, 2001).

Because pollen release and stigmatic acceptance take place at different times in dichogamy, pollinators undoubtedly pose an important aspect for dichogamous species. Pollination behaviors of protandrous and protogynous flowers exhibit a certain level of variation. Sargent and Otto (2004) studied the role of pollinators in evolution of dichogamy types, and found no evidence of any direct effect of pollinators on the evolution of dichogamy types. However, they concluded that dichogamy types do affect the evolution of pollination behavior.

Proterandry is more common in species with biotic pollination and the pollinator agents are usually birds and bees (Behrens, 1885). The protandrous flowers of *H. annuus* L. exhibit biotic pollination behavior and the pollinator agents are usually the bees. Bees roam in sunflower capitulums in order to collect nectar and provide pollination by roaming different plants. Proterogyny is more common among species that exhibit abiotic pollination and the pollinator agent is usually the wind (Müller, 1883; Henslow, 1888). However, biotic agents such as insects and yellow bees may also serve pollination in protogynous flowers. When the biology of floral pollination is investigated, proterogyny is seen to be 6 times more prevalent than proterandry in species with abiotic pollination while proterandry is 2 times more common among species with biotic pollination (Bertin and Newman, 1993).

Geographic location also has a substantial effect on dichogamy and the distribution of dichogamy among plants may vary across arctic, moderate, and tropical regions. Dichogamy is frequently seen among plants in tropical regions. A high rate of adichogamy is seen in arctic

regions (Bertin and Newman, 1993), and proterogyny is relatively common among the limited number of dichogamous species. Proterandry is commonly observed among plants in tropical regions. This may be partially related to the accelerated maturity of stamens due to warm weather, leading to the start of pollen release in a short period of time.

The habitat and ecological conditions of the plant also affect dichogamy. Because certain dichogamy types are associated with certain plant families, it is difficult to interpret dichogamy types by ecological conditions. However, studies have been conducted to provide an explanation of this aspect by phylogenetic relationships. While alpine species are commonly dichogamous, adichogamy is common in desert species. The dichogamy commonly seen in alpine species is usually in the form of proterogyny. Henslow (1888) found that 30.8% of 1194 species from all habitats were protogynous while 55.5% of the 17 alpine species protogynous. However, proterogyny is still the most common among aquatic species. Furthermore, the species that most commonly exhibit proterandry are distributed across shrub habitats. The dichogamy tendency may also change according to the age of trees. For example, dichogamy is more common among young walnut trees.

The prevalence of dichogamy may also vary according to different sexual systems. Gynodioecious, gynomonoecious, trioecious species usually tend to be protandrous. As it contains both hermaphrodite and female flowers, *H. annuus* L. is defined as a gynomonoecious plant and its protandrous nature supports this data (Çetinbaş and Ünal, 2012). Darwin (1888) contributed to this criterion by commenting that "all gynodioecious plants exhibit dichogamy". Androdioecious species mostly tend to be protogynous. Apart from these, proterandry and adichogamy is seen at nearly equal rates in all of the other sexual systems.

Function of Dichogamy

Although the function of dichogamy has not been fully understood, there are some hypotheses regarding its evolution (Routley, Bertin and Husband, 2004). The most common hypothesis suggests that dichogamy is a mechanism which decreases inbreeding and increases cross-fertilization by limiting the pollen transfer between flowers (Darwin, 1876). However, some investigators found no evidence to support this hypothesis and challenged this interpretation (Hossaert-McKey and Bronstein, 2001). In a study on 4000 species, Bertin (1993) showed the presence of dichogamy in 73% (55 families) of 160 self-incompatible species and 75% (89 families) in 673 self-compatible species. Self-incompatible plants lack the ability of self-fertilization, and the suggestion that "dichogamy is only a mechanism to avoid self-fertilization" in this hypothesis therefore appears to be inconsistent. Because dichogamy has been seen nearly at the same rate among self-compatible and self-incompatible species (Lloyd and Webb, 1986; Bertin, 1993).

Some investigators, on the other hand, have expressed that the effect of dichogamy on self-fertilization may vary according to the type of dichogamy (Godley, 1955; Marilaun, 1895; Lloyd and Webb, 1986; Lloyd and Yates, 1982; Palmer and Travis, 1989; Pijl, 1978; Wyatt, 1983). Bertin (1993) has reported that proterogyny may be a mechanism which leads to some decrease in self-fertilization, however stated that there is no evidence to support the same effect for proterandry. This is related to the fact that the stigma is not a recipient when the pollen reaches maturity, and therefore the pollen can not meet its own stigma and may be obliged for cross-fertilization in proterogyny. On the other hand, self-fertilization may be seen in proterandry if the pollen persists and maintains viability until stigma divide in two parts. Furthermore, self-pollination is substantially prevented in presence of complete dichogamy. However, if dichogamy is not completed, there may be

different outcomes for proterandry and proterogyny, and self-pollination may occur (Faegri and Pijl, 1979; Webb, 1981; Bawa and Beach, 1981).

Due to its protandrous flowers, *H. annuus* L. may be defined as a self-incompatible plant. For this reason, it may be suggested that dichogamy (protandrous dichogamy) leads to obligatory cross-pollination in *H. annuus* L. by limiting pollen transfer (Çetinbaş and Ünal, 2012). That is why *H. annuus* L. mostly exhibits cross-fertilization.

However, self-fertilization may also occur in *H. annuus* L. due to the presence of incomplete proterandry. Because the reproductive stage of the stamen and the female reproductive stage overlap for a short period of time, self-fertilization may occur even if it is a low possibility. Apart from this, because the pollen grains may maintain viability for a while after their release, they may be stored on the stigma until the stigma is able to accept pollen and the pollen may fertilize the pistil when stigma gains reproductive activity. Therefore, the possibility of dichogamy to decrease self-fertilization should be assessed by considering different parameters.

Another hypothesis regarding the function of dichogamy is the decreased interference between male and female sex organs (Wyatt, 1983; Lloyd and Webb, 1986; Bertin, 1993; Harder *et al*., 2000; Barrett, 2002) the evolutionary stability strategy which increases the male-female reproductive success (Wiklund and Fagerstrom, 1977; Zonneveld and Metz, 1991; Carvalho *et al*., 1998; Castillo and Nunez-Farfan, 2002). This hypothesis has been more widely accepted compared to the others and has been considered to be more effective than other hypotheses.

Hermaphroditism is the coexistence of male and female sex organs and is the most common form of reproductivity among floral plants. Coexistence of two sexes in a singe flower increases the pollen mobility and accumulation by pollinators (Barrett, 2002), and provides reproductive assurance (Fenster and Marten-Rodriguez, 2007). However, hermaphroditism leads to sexual interference (Barrett, 2002). Hermaphrodite plants undergo selective pressure to separate male and female functions (Charlesworth and Charlesworth, 1987) and to decrease sexual interference (Lloyd and Yates, 1982) in order to reduce reproductive depression.

Sexual interference is not observed in dioecious species. The intensity of sexual interference may be decreased in unisexual floral species or in those where male and female function are separated temporally (dichogamy) or spatially (herkogamy).

Sexual interference may be crucial during the periods when the pollen and stigma are expressed at the same time in the same flower in hermaphrodites. It reduces the female compatibility by decreasing the cross-fertilization success and reduces the male compatibility by decreasing pollen release to other individuals (Harder and Wilson, 1998). This eventually leads to reduced gametes and productivity. On the other hand, if self-pollen accumulates on the stigma, this leads to reduced pollen quality and the pollinators carry the pollen with decreased quality to other individuals (Harder and Wilson, 1998).

Particularly in hermaphrodite species, expression of male and female functions at different times due to dichogamy reduces sexual interference, leading to better productivity and better gamete production. Complete dichogamy is particularly more successful in prevention of interference as it completely separates male and female functions. However, considering that incomplete dichogamy is more prevalent than complete dichogamy, we may see that this mechanism does not fully reflect the evolution of dichogamy. The gain of reproductive activity in the stamen before the pistil in hermaphrodite flower of *H. annuus* L. separates male and female functions, and decreases sexual interference. However, this is not very successful in the *H. annuus* L. flower with incomplete proterandry. This is associated with the overlap between male and female

functions even if it lasts for a short period of time.

In self-incompatible species, physiological restrictions prevent self-fertilization and self-pollination (Richards, 1997) and majority of investigators therefore accept that dichogamy reduces sexual interference (Waites and Agren, 2006).

Another hypothesis suggests that dichogamy (particularly proterandry) may occur through a choice favoring early or extended pollen presentation (Bawa and Beach, 1981; Lloyd and Webb, 1986; Webb, 1981). The possibility of fertilization is higher during the early male phase. Therefore, early pollen presentation due to proterandry may increase the pollinator visits in a single plant, causing pollinators to be already present when stigma is fully expressed (Gilbert, 1975). And if dichogamy is selected for extended pollen presentation, incomplete proterandry remains in the selection mode.

Another hypothesis suggests that dichogamy may reflect the different compatible positions for pollen transfer and acceptance in species with increased height or degree of anther exertion observed between two sexual phases (Marilaun, 1895; Lloyd and Webb, 1986). In species that pollinate by animals, the pollen and stigma should touch the same part of the animal and generally presentation in the same position should be selected in a single flower. There is no such restriction in plants which pollinate by wind or water; they do not need to be in the most appropriate position or condition for pollen transfer and acceptance. Dichogamy is thought to allow the pollen and stigma presentation in such cases where the pollen and stigma are located in different positions on a plant.

Molecular Mechanism of Dichogamy

There are no studies on the molecular mechanism of dichogamy. However, Henslow (1888), Willemstein (1987), Wyatt (1983), Faegri and Pijl (1979) suggested that intrafloral proterandry reflects the natural centripetal development of floral elements, causing proterandry to be more common. When dichogamy is evaluated in terms of floral organ development in light of this estimation, the ABC model formulated by Coen and Meyerowitz in 1991 may be considered as dominant on dichogamy.

According to the ABC model, 3 genes affect floral organ development with their individual effects or through combinations with other genes. These genes are referred to as A, B and C. Expression of gene A produces the cephal while the expression of gene C produces the carpel. Co-expression of gene A and B lead to the formation of petals whereas co-expression of gene B and C lead to the formation of stamens. In light of this information, the molecular mechanism of dichogamy may be interpreted with an example where the stamen expressing gene B and C are the first to be activated concurrently in a protandrous flower. Subsequently, gene B loses its activity and the female phase starts as gene C remains active alone. However, this interpretation is applicable only at the level of intrafloral dichogamy.

Conclusion

Dichogamy is the maturation of male and female reproductive organs at different times. It is an evolutionary stability strategy to increase male and female reproductive success by reducing the interference between sex organs and also a mechanism which partially increases the rate of cross-fertilization.

The present study is a review of previous studies on dichogamy and types and functions of dichogamy. Types of dichogamy have been described by evaluating the dichogamous characteristics of *H. annuus* L., and types of dichogamy have been depicted schematically in order to clarify the subject. Interpretations have been made regarding the mechanism of dichogamy and the discussions on evolutionary mechanisms have been evaluated.

The present study is considered to be possibly effective to describe and types of dichogamy and to contribute to further

studies on it. There are a limited number of studies on dichogamy, and the present study is expected to guide the definition and studies on this subject.

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